

Ontogenetic change in the diet of *Semaprochilodus insignis* (Characiformes: Prochilodontidae) during migration between two limnologically distinct environments in the Amazon Basin

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Semaprochilodus insignis is an Amazonian migratory fish species, moving in large shoals between white- and black-water rivers. It has long been classified as a detritivorous fish. However, it is possible that the trophic plasticity of *S. insignis* could be higher than previously assumed. The objective of this study was to investigate the relative contributions of autotrophic energy sources to the diet of *S. insignis* in the Negro and Solimões rivers and to determine if the species undergoes an ontogenetic change in the diet. We found variations between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *S. insignis* between the rivers. In the Negro River, periphyton (84%) was the principal energy source for adults, while juveniles in the Solimões River foraged predominantly on terrestrial plants/ C_3 macrophytes (50%) and phytoplankton (42%). These variations in isotopic signatures are likely associated with migratory movements of *S. insignis* at different life stages and hydrological periods. Instead of the previously assumed dietary classification, we suggest that *S. insignis* varies its diet ontogenetically, with adults acting as illiophagous in black-water while the young are detritivorous in white-water rivers. The results show that this species creates complex links between food chains, thus emphasizing the importance of conserving flooded areas.

Keywords: Autotrophic sources, Illiophagous, Negro River, Solimões River, Stable isotopes.

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Semaprochilodus insignis é uma espécie de peixe migratório da Amazônia, movendo-se em cardumes entre rios de água branca e preta. Tem sido classificado como um peixe detritívoro-iliófago. Porém, é possível que a plasticidade trófica de *S. insignis* seja maior do que se supunha. O objetivo deste estudo foi investigar as contribuições relativas de fontes de energia autotróficas para a dieta do *S. insignis* nos rios Negro e Solimões e se a espécie muda ontogeneticamente a sua dieta. Encontramos variações entre os valores de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ de *S. insignis* entre os rios: Negro, o perifíton (84%) foi a principal fonte de energia para adultos, enquanto para os juvenis do rio Solimões, foram predominantemente as plantas terrestres/macrófitas C_3 (50%) e fitoplâncton (42%). Essas variações nas assinaturas isotópicas provavelmente estão associadas a movimentos migratórios do *S. insignis* em diferentes estágios da vida e períodos hidrológicos. Ao invés da classificação alimentar previamente assumida, sugerimos que o *S. insignis* varie sua dieta ontogeneticamente, os adultos são iliófagos em águas negras, enquanto os jovens são detritívoros em rios de águas brancas. Os resultados demonstram que essa espécie promove ligações complexas entre as cadeias alimentares enfatizando, dessa forma, a importância da conservação das áreas inundadas amazônicas.

Palavras-chave: Fontes autotróficas, Iliófagos, Isótopos estáveis, Rio Negro, Rio Solimões.

INTRODUCTION

The rivers and floodplains of the Amazon River basin contain distinct physical, chemical, and biological characteristics (Sioli, 1991), which in turn contribute to the large diversity of habitats sustaining the world's greatest biodiversity of freshwater fish (Lowe-McConnell, 1999). Some of these fish species are also commercially important, including *Semaprochilodus insignis* (Jardine, 1841), a migratory fish that moves in large shoals between distinct aquatic habitats of black- and white-water river systems (Ribeiro, 1983; Benedito-Cecilio, Araújo-Lima, 2002). These migratory movements are directly correlated with seasonal variations in water level, which are driven by the monomodal hydrological flood pulse of the Amazon River and its tributaries, as well as with the life stage of the species (Ribeiro, 1983; Guerreiro *et al.*, 2020), which can be defined as adults when the individuals reach 22.3 cm of standard length and two years-old (Vieira *et al.*, 1999; Vieira, 1999, 2003).

At the beginning of the rising-water period, *S. insignis* adults migrate from black-water habitats to white-water systems to lay their eggs in running waters, before returning to seasonally-flooded forests (locally called igapó) of black-water rivers to feed intensively for three months (Ribeiro, 1983). In white-water systems, the larvae are carried by currents into floodplain lakes (locally called várzea), where nutrient-rich vegetation both protects and feeds the fry during the juvenile stage (Leite *et al.*, 2002; Lima, Araújo-Lima, 2004; Mounic-Silva, Leite, 2013). Várzeas are the most productive freshwater systems in the Amazon basin (Melack, Forsberg, 2001), with a diversity of aquatic habitats, including rooted and floating banks of macrophytes, offering

important refuge for juvenile fish (Sánchez-Botero, Araújo-Lima, 2001; Leite, Araújo-Lima, 2002). After successful growth and juvenile development, *S. insignis* juveniles migrate to the flooded forest habitats of black-water rivers to complete the recruitment stage and grow into adults (Ribeiro, 1983).

Much of the feeding of *S. insignis* has been focused on detritus that originates from varying autotrophic energy sources, including terrestrial shrubs and trees, C₃ and C₄ macrophytes, periphyton, and phytoplankton (Araújo-Lima *et al.*, 1986; Fernández, 1993; Yossa, Araújo-Lima, 1998; Silva-Prado *et al.*, 2019). Previous work focused on species found in the várzea floodplains using an analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes indicated that phytoplankton was the principal autotrophic energy source to *S. insignis* (Fernández, 1993; Forsberg *et al.*, 1993; Benedito-Cecilio *et al.*, 2000). Benedito-Cecilio, Araújo-Lima (2002) showed that $\delta^{13}\text{C}$ values of *S. insignis* collected in várzeas are more enriched isotopically than in black-water environments. However, these authors employed a simple mass-balance mixing model using only $\delta^{13}\text{C}$ signatures instead of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, a technique which is thus less accurate for determining the relative contributions of basal energy sources to consumers. In addition, Benedito-Cecilio, Araújo-Lima (2002) did not consider the variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at different life stages during migratory movements, so this work likely does not present a complete picture of consumption by and the overall impact of *S. insignis* in this region.

The objective of the present study was to determine the relative contributions of autotrophic energy sources to the diet of *S. insignis* in the lower Solimões River (white-water) and Negro River (black-water) in low and high-water periods, respectively, based on the known isotopic signatures of basal energy sources in the two systems. The determinations of these contributions therefore enable us to investigate ontogenetic changes of the diet of *S. insignis*. In this study we specifically examined how this migratory fish creates links between food chains using different energy sources in limnologically unique systems of the Amazonian flooded areas during their life cycle. A broader aim of this work was to further comprehend and demonstrate the ecological complexity and importance of conserving the flooded areas of Central Amazonia.

MATERIAL AND METHODS

Study area. The study was conducted in the lower reaches of the Negro and Solimões rivers, close to the confluence of both rivers. The upper limit in the Negro River was the Anavilhanas Archipelago, located approximately 40 km from the confluence with the Solimões River, while the upper limit in the Solimões River was Paciência Island, situated close to 50 km upriver (Fig. 1).

The Negro River is classified as a black-water river, with low pH (3.89–6.07; Küchler *et al.*, 2000) due to humic acids leached from phenol-containing vegetation, few suspended solids (11.4 mg L⁻¹; Küchler *et al.*, 2000), and poor primary productivity (Goulding *et al.*, 1988). The Anavilhanas Archipelago covers an area of 3,504 km² and is composed of flooded forests, islands, lakes, channels, and sandy beaches (Leenheer, Santos, 1980; Latrubesse, Franzinelli, 2005), with approximately 100 km² seasonally flooded by the Negro River (Franzinelli, Igreja, 2002; Nakazono, Piedade, 2004). In



FIGURE 1 | Location of study areas (in white line) and collection points (red triangles) in Amazonas, Brazil. QGIS 2.18 and Bing © 2019 Microsoft Corporation Geographic SIO.

comparison, the Solimões River is a white-water river with a high sediment load ($7.7\text{--}8.6\text{ mg L}^{-1}$; Küchler *et al.*, 2000), which generates high primary production (Sioli, 1991; Melack, Forsberg, 2001). Numerous lakes on Paciência Island are flooded seasonally by the Solimões River, as are large areas of várzea forest.

Data collection. *Semaprochilodus insignis* were collected in the Anavilhanas Archipelago ($02^{\circ}47'S\ 60^{\circ}46'W$, black water environment) in May 2015 during the high-water period (adult specimens, $SL = 24.4 \pm 1.35\text{ cm}$) and on Paciência Island ($03^{\circ}18'S\ 60^{\circ}12'W$, white water environment) in January 2016 at low-water period (juvenile specimens, $SL = 16.73 \pm 0.73\text{ cm}$), to coincide with the migratory cycle of the species. During the rising-water each year, *S. insignis* adults migrate from black-water rivers to spawn in white-water rivers. After spawning they return to black-water environments. The eggs, larvae and juveniles of this species develop in white-water environments, remaining until the next rising-water, when they migrate to black-water rivers, completing their life cycle in these environments (Ribeiro, 1983; Leite, Araújo-Lima, 2002).

Oliveira (2003) showed that isotopic turnover in the Amazonian fish *Colossoma macropomum* (Cuvier, 1816) occurred in 85 days. As carbon turnover within an organism is associated with their growth rate (Manetta, Benedito-Cecilio, 2003), a fast-growing species like *S. insignis* with a K value of 0.5 (Vieira, 1999; Vieira *et al.*, 1999) would therefore likely have a faster turnover rate than *C. macropomum*, which has a K value of only 0.16 (Villacorta-Correa, 1997). Sacramento *et al.* (2016) estimated a rate of carbon

turnover in the *Prochilodus lineatus* (Valenciennes, 1837) muscle of 13.9 days for a C₃ and C₄ plant-based diet. The six-month time interval between the sampling periods was considered to be sufficient to avoid overlapping of isotopic signals on fish migrating between locations.

Semaprochilodus insignis individuals were captured with gillnets placed perpendicularly in the water around floating macrophyte stands daily from 05:00–07:00 each morning. We caught these fish using gillnets with mesh size of 30 mm which are 15 m in length and 5 m wide between opposite nodes. In total, 15 fish were collected in each collection site/system, placed on ice, and transported to the Ichthyology Laboratory at Universidade Federal do Amazonas (UFAM), Manaus, Brazil. There, each fish was measured for standard length (SL) in centimeters (cm) and weighed in grams (g). One sample of dorsal muscle tissue (1.73 ± 0.28 g) from each fish was also collected and stored in Eppendorf tubes in the freezer. Following this subsampling, samples were removed from the tubes and dried on petri dishes in an oven at 50 °C for 72 h, stored once again in Eppendorf tubes.

Given that *S. insignis* has been known to be a detritivorous fish (Goulding, 1980; Fernández, 1993; Yossa, Araújo-Lima, 1998) and that until now detritus of the Negro River has not been characterized isotopically, a total of nine samples from benthic substrates were collected in May 2015 using a dredge. Leaves, roots, bark, wood and sand were all removed to obtain a detrital sample as pure as possible. In the laboratory, all samples were heated at 50 °C for 72 h, placed in Eppendorf tubes, and sent to the Virginia Military Institute, Lexington (USA) for final preparation for isotopic analysis. For detritus from the Solimões River, isotopic data was used from Oliveira (2003) and Santos (2009).

Isotopic data of autotrophic energy sources found in the Solimões River were collected from Oliveira *et al.* (2006), Santos (2009), and Costa *et al.* (2017), as well as from the project titled “The biology and ecology of várzea fish species: conservation strategies for sustainable fisheries in the Amazon” (MCT/CNPq/PPG7 # 557060/2005–2). For the Negro River, isotopic data of basal sources were used from Thomé-Souza (2005), Marshall *et al.* (2008), and Marshall (2010), in Tab. 1. Oliveira *et al.* (2006) obtained the samples of phytoplankton by filtering collected water through a 53 µm mesh net to eliminate zooplankton and large particles of detritus, and again through a 25 µm mesh net to retain the fine particulate matter (live phytoplankton, organic detritus, and bacteria). Santos (2009) collected samples with a 20 µm phytoplankton net and then filtered through 20 µm and 10 µm mesh. Thomé-Souza (2005), Marshall *et al.* (2008), and Marshall (2010) collected periphyton samples through the separation of colonies from debris and substrates. In the Negro River, phytoplankton production is extremely low, so no data on this source has been obtained. The C₄ macrophytes only occur in the Solimões River.

Laboratory analyses. After oven drying, muscle tissue and sediment samples were ground to a fine powder using a mortar and pestle. For isotopic analysis, 1.0 ± 0.2 mg sub-samples were analyzed in the Central Appalachians Stable Isotope Facility in Frostburg, Maryland (USA) using a Carlo Erba NC2500 elemental analyzer with a Thermo Delta V isotope ratio mass spectrometer. The isotopic ratios were expressed using delta notation (δ) in parts per thousand (‰): $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = ((R_{\text{sample}}/R_{\text{standard}}) - 1)$

$\times 1000$, where $R_{\text{sample}}/R_{\text{standard}}$ refer to the $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratios, respectively. The reference standards used were Vienna PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Analytical precision was estimated at $\pm 0.12\text{‰}$ and $\pm 0.11\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Data analysis. All the analyses were conducted using R software, version 3.2.5 (R Development Core Team, 2016). Statistical significance of all tests was established as $\alpha = 0.05$. A Student t-test was applied to compare the average values of $\delta^{13}\text{C}$ between *S. insignis* from the Negro and Solimões River. As the residuals of the analysis using $\delta^{15}\text{N}$ was deemed to be heterocedastic, a *U Mann-Whitney* test was applied to compare the average values of $\delta^{15}\text{N}$ in *S. insignis* from the two river systems. Two two-way ANOVAs were applied to compare the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the autotrophic energy sources from the Solimões and Negro rivers, including forest leaves, C_3 macrophytes, periphyton, and detritus. Post-hoc comparisons for observed means were performed with a Tukey test.

The Stable Isotope Mixing Model in R (SIMMR; Parnell, Inger, 2016), based on Bayesian statistics, was used to evaluate the relative contributions of autotrophic energy sources to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *S. insignis* in the two systems and to evaluate the relative contributions of autotrophic energy sources in the detritus. Bayesian statistics incorporates more sources of variability within the model, while allowing multiple energy sources to generate potential mixture solutions as true probability distributions. The trophic fractionation factors used were $\delta^{13}\text{C} = 1.0\text{‰}$ (standard deviation = 1.1‰) and for $\delta^{15}\text{N} = 2.3\text{‰}$ (standard deviation = 1.3‰) (Molina *et al.*, 2011).

The nitrogen isotopic values were used to estimate the trophic position (TP) of *S. insignis* individuals of each environment using the following equation: $\text{TP} = [1 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{reference}}) / \text{trophic fractionation value}]$ (Post, 2002), where 1 is the trophic level of the organism used as our $\delta^{15}\text{N}_{\text{reference}}$. In this study we used the mean $\delta^{15}\text{N}$ value of periphyton as a reference with a trophic fractionation value of 2.3‰ (Post, 2002; Molina *et al.*, 2011). Periphyton is the most appropriate reference due to its role as a primary producer fulfilling the conditions proposed by Post (2002).

RESULTS

Relative contributions of autotrophic energy sources to the *Semaprochilodus insignis*. The potential autotrophic energy sources in the two systems that can contribute to the isotopic composition of *S. insignis* are shown in Tab. 1. In the Negro River, there were significant differences between the average $\delta^{13}\text{C}$ values of the autotrophic energy sources ($F = 10.89$; $p < 0.05$; $gl = 2$), with the exception of the C_3 macrophytes that were not significantly distinct isotopically from the forest leaves (Fig. 2A; Tab. 1). The average $\delta^{15}\text{N}$ values of the sources were not statistically different.

In the Solimões River, there were significant differences between the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the autotrophic energy sources ($\delta^{13}\text{C}$: $F = 459.4$; $gl = 4$ $p < 0.05$; $\delta^{15}\text{N}$: $F = 9.00$; $p < 0.05$; $gl = 4$) (Fig. 2B; Tab. 1). While C_4 macrophytes exhibited the most enriched $\delta^{13}\text{C}$ value, phytoplankton exhibited the most depleted average value. The periphyton in the Solimões River had the most enriched average $\delta^{13}\text{C}$ value between C_3

plants, while in the Negro River it was the most depleted.

In both systems, the average $\delta^{13}\text{C}$ values of detritus were similar to those of forest leaves and C_3 macrophytes, while the average $\delta^{15}\text{N}$ values were most similar to those of periphyton (Fig. 2; Tab. 1). Considering that forest leaves and C_3 macrophytes were not statistically different from each other in terms of their average $\delta^{13}\text{C}$ values, they were grouped together as one plant source called Group of Leaves + Macrophytes in the mass balance mixing model.

Bayesian analysis using the SIMMR model indicated that detritus of the Negro River had an isotopic composition of 82% Group of Leaves + Macrophytes and 18% periphyton (Fig. 3A), while in the Solimões River phytoplankton contributed 53%, Group of Leaves + Macrophytes 32%, periphyton 10% and C_4 macrophytes with 5% (Fig. 3B).

There were different values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *S. insignis* from the Negro and Solimões rivers (For $\delta^{13}\text{C}$, $F = 376.7$; $p < 0.05$; $g_l = 1$; For $\delta^{15}\text{N}$, $W = 225$; $p < 0.05$). The $\delta^{13}\text{C}$ values were more depleted and $\delta^{15}\text{N}$ values more enriched in specimens from the Negro River ($-37.23 \pm 0.83\text{‰}$; $8.37 \pm 0.81\text{‰}$) compared to those from the Solimões River ($-30.06 \pm 1.17\text{‰}$; $6.02 \pm 0.30\text{‰}$). The trophic positions estimated through $\delta^{15}\text{N}$ for *S. insignis* from the Negro and Solimões rivers were 3.27 and 1.48, respectively.

The SIMMR mixing model showed that periphyton contributed 84% to the autotrophic energy source composition of *S. insignis* in the Negro River, with Group of Leaves + Macrophytes contributing only 16%. In comparison, Group of Leaves + Macrophytes (50%) and phytoplankton (42%) were the principal autotrophic energy sources for *S. insignis* in the Solimões River, while periphyton and C_4 macrophytes contributed only 6% and 2%, respectively (Fig. 4).

TABLE 1 | Means (\bar{x}) and standard deviations (SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of autotrophic energy sources of the Negro and Solimões rivers derived from the literature. n = number of samples, followed by reference number. 1– Oliveira *et al.* (2006); 2– Santos (2009); 3– Costa *et al.* (2017); 4– database of project biology and ecology of várzea fish species: conservation strategies for sustainable fisheries in the Amazon” (MCT/CNPq/PPG7 # 557060/2005-2); 5– Thomé-Souza (2005); 6– Marshall *et al.* (2008); 7– Marshall (2010). The differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the sources of energy of the Solimões River are represented by lowercase letters, as well as in the autotrophic sources in the Negro River. The differences of $\delta^{13}\text{C}$ between the sources of energy of the Negro River and the sources of energy of the Solimões River are represented by uppercase letters.

Plant Sources	Negro River			Solimões River		
	n	$\bar{x}\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	$\bar{x}\delta^{15}\text{N} \pm \text{SD} (\text{‰})$	n	$\bar{x}\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	$\bar{x}\delta^{15}\text{N} \pm \text{SD} (\text{‰})$
Forest leaves	15 ^(5,6,7)	$-30.82 \pm 2.67^{\text{aA}}$	1.96 ± 3.38	7 ^(1,2,3)	$-29.14 \pm 1.15^{\text{aA}}$	$4.03 \pm 1.49^{\text{ab}}$
C_3 macrophytes	5 ⁽⁷⁾	$-29.72 \pm 3.10^{\text{aA}}$	3.03 ± 3.66	14 ^(1,3,4)	$-29.43 \pm 1.02^{\text{aA}}$	$3.18 \pm 2.61^{\text{b}}$
Periphyton	15 ^(5,6,7)	$-37.34 \pm 4.81^{\text{bA}}$	3.15 ± 2.85	4 ^(2,4)	$-23.21 \pm 0.07^{\text{bB}}$	$4.92 \pm 0.13^{\text{abc}}$
Phytoplankton	-	-	-	11 ^(1,2,4)	$-34.46 \pm 1.63^{\text{c}}$	$6.26 \pm 0.53^{\text{ac}}$
C_4 macrophytes	-	-	-	11 ^(1,2,3,4)	$-12.51 \pm 0.97^{\text{d}}$	$7.42 \pm 1.80^{\text{c}}$
Detritus	9	$-29.24 \pm 0.90^{\text{aA}}$	3.47 ± 0.40	5 ^(1,2)	$-30.89 \pm 1.19^{\text{aA}}$	$4.90 \pm 0.69^{\text{abc}}$

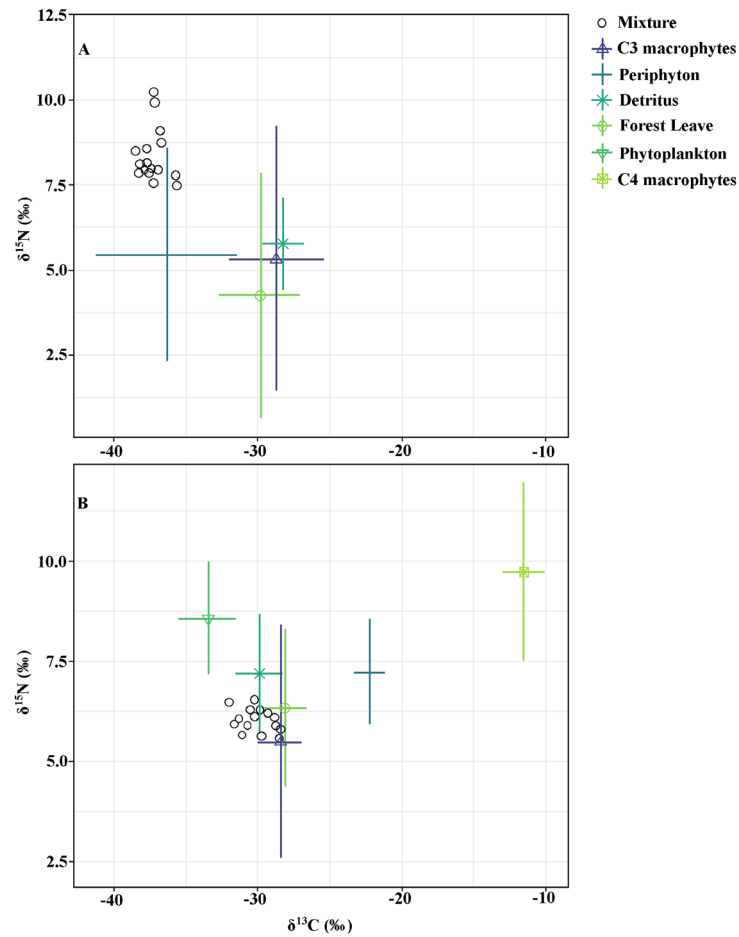


FIGURE 2 | Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations of the autotrophic energy sources and *Semaprochilodus insignis* muscle tissue (Mixture), in Amazonas, Brazil. **A.** Negro River (*S. insignis* adults, $n = 15$); **B.** Solimões River (*S. insignis* juveniles, $n = 15$).

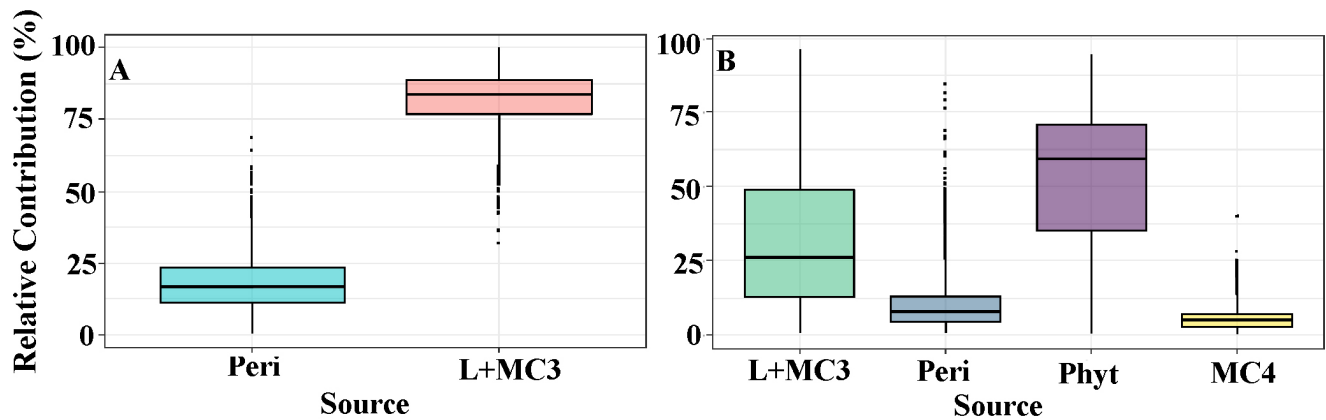


FIGURE 3 | Relative contributions (%) of autotrophic energy sources in the detritus collected from two Amazonian rivers, in Amazonas, Brazil. **A.** Negro River; **B.** Solimões River. L+MC3 = Group of leaves + Macrophyte; Peri = Periphyton; Phyt = Phytoplankton; MC4 = C₄ Macrophytes.

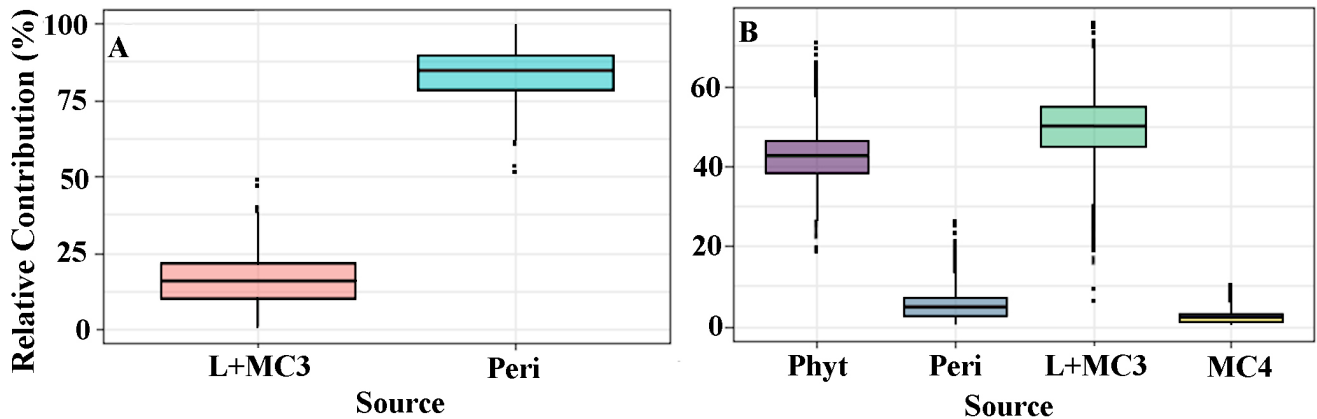


FIGURE 4 | Relative contributions (%) of autotrophic energy sources of *Semaprochilodus insignis* collected from two Amazonian rivers, in Amazonas, Brazil. **A.** Negro River; **B.** Solimões River. L+MC3 = Group of leaves + Macrophyte; Peri = Periphyton; Phyt = Phytoplankton; MC4 = C₄ Macrophytes.

DISCUSSION

Relative contributions of autotrophic sources to the *Semaprochilodus insignis*. *Semaprochilodus insignis* has long been considered a detritivore, consuming basal material deposited on substrates like submerged rocks, tree trunks, leaf litter, and vegetation at the margins of lakes and rivers, including periphyton that is possibly ingested by scraping from the substrate.

In this research it is understood that detritus is a mixture of more than one autotrophic energy source, a set of living and dead material composed of fungi, bacteria, macroinvertebrates, algae, and decomposed organic matter from aquatic and terrestrial plants. In the Solimões River, detritus is composed of phytoplankton and the previously defined Group of Leaves + Macrophytes. Similarly, the Group of Leaves + Macrophytes and phytoplankton were the principal autotrophic energy sources for *S. insignis* juveniles in this environment, underscoring the importance of detritus for this species. Terrestrial plants contribute significantly to the carbon pool in white-water systems, producing an estimated quantity of 11.35 tCha⁻¹a⁻¹, while C₃ macrophytes produce approximately 24.91 tCha⁻¹a⁻¹ (Melack, Forsberg, 2001). This material is predominantly produced during the high-water period and begins to decompose in the receding-water period (Silva *et al.*, 2009; Piedade *et al.*, 2010). At the end of the low-water period, a large amount of detritus has been generated from the breakdown of both terrestrial matter and aquatic macrophytes, driving carbon flow for metazoan production and sustenance for consumers like *S. insignis*.

Even though phytoplankton productivity in the Solimões River floodplains is comparatively modest at 0.68 tCha⁻¹a⁻¹ (Melack, Forsberg, 2001; Melack *et al.*, 2009), this energy source has high nutritional quality in comparison to vascular plants, demonstrating its importance for *S. insignis* and other species (Araújo-Lima *et al.*, 1986; Hamilton *et al.*, 1992; Forsberg *et al.*, 1993; Benedito-Cecilio *et al.*, 2000; Lewis *et al.*, 2001; Mortillaro *et al.*, 2015).

The periphyton contribute only 6% to the biomass of *S. insignis* juveniles, which is likely due to the differences in collection times between *S. insignis* and autotrophic

sources, since there may be variation in the isotopic composition of the periphyton during the hydrological cycle. In the low-water season, the productivity of the periphyton is generally low due to the turbidity caused by resuspension of sediments (Engle, Melack, 1989).

The production of C₄ macrophytes in várzea floodplains is between 22 to 80 t.ha⁻¹ (Piedade *et al.*, 1991; Junk, Piedade, 1993); despite this, these macrophytes contributed only 2% to *S. insignis* juveniles biomass. High primary production levels are then clearly disproportionate to its selectivity as an energy source by *S. insignis* and other fish species (Hamilton *et al.*, 1992; Forsberg *et al.*, 1993; Oliveira *et al.*, 2006; Jepsen, Winemiller, 2007; Mortillaro *et al.*, 2015). This is likely due to its low nutritional quality and high lignin content, rendering energy assimilation difficult (Forsberg *et al.*, 1993; Oliveira *et al.*, 2006; Mortillaro *et al.*, 2015).

In the Negro River, periphyton were the main energy source of *S. insignis*. However, the Leaves + Macrophytes Group were the energy sources that predominantly contributed to the detritus collected in the benthic substrates of the Negro River. This indicates that *S. insignis* exploits the periphyton through other substrates, taking advantage of the high-water period, when the biomass of this energy source in the Negro River is greater (Rai, Hill, 1984; Díaz-Castro *et al.*, 2003, 2008). Many studies have shown the importance of algae as dietary components, as well as their dominance as autotrophic energy sources sustaining aquatic food chains in black-water systems (Hamilton *et al.*, 1992; Lewis *et al.*, 2001; Thorp, Delong, 2002; Jepsen, Winemiller, 2002, 2007; Thomé-Souza, 2005; Marshall *et al.*, 2008; Marshall, 2010; Junk *et al.*, 2011). However, it is necessary to consider the caveats of this result, as some sources, such as phytoplankton and C₄ macrophytes, were not included to the mixing model. These two sources of energy are almost absent in black water rivers, like the Negro River (Lewis, 1998; Sioli, 1991; Thomé-Souza, 2005), making collection difficult in this environment.

Illiohagous fish are those that explore benthos or periphyton, ingesting fine particulate sediment together with micro-organisms and unicellular algae, while detritivorous fish are those that exploit detritus with vegetative components in earlier stages of decomposition (Agostinho *et al.*, 1997). Average values for these trophic habits were calculated by Benedito-Cecilio *et al.* (2002), with illiohagous fish displaying a trophic position of 3.5 and detritivorous fish 2.3. Although the literature generally indicates that *S. insignis* is a detritivorous species, the dietary characteristics and related trophic position revealed by our study suggest that there is an ontogenetic shift in the dietary preferences of *S. insignis*, as those in the Negro River (TP = 3.27) should be considered as illiohagous, while juveniles in the Solimões River (TP = 1.48) are detritivorous.

Movements and ontogenetic change in the diet of *Semaprochilodus insignis*.

The movements associated with ontogenetic development in aquatic organisms are driven by a quest for maximum survivability, which includes finding refuge from predators, taking advantage of the best food resources available and ensuring optimal protection of eggs and larvae (Winemiller, Jepsen, 2005). For a species like *S. insignis*, these movements are correlated with reproductive migration. The adults migrate from black-water flooded forest habitats to white-water floodplains to lay their eggs, as these latter environments guarantee the survival and growth of their young (Ribeiro, 1983).

This migration occurs during the rising-water period, which facilitates the dispersion and transport of eggs into rich floodplains at the edge of the main channel (Ribeiro, Petrere-Junior, 1990).

During the rising-water and high-water periods in the Solimões River, there is high primary productivity of many autotrophic energy sources, including terrestrial matter, C₃ and C₄ macrophytes, phytoplankton and periphyton, which use the macrophytes and other submerged substrates for colonization (Melack, Forsberg, 2001). However, in the receding-water and low-water periods, the gradual retreat of water causes the decomposition of many aquatic plants, which in turn generates high concentrations of organic and inorganic nutrients and sediments (Winemiller, Jepsen, 2005; Piedade *et al.*, 2010).

The results of this study show that *S. insignis* juveniles in the Solimões River assimilate autotrophic energy predominantly derived from terrestrial plants and C₃ macrophytes, as well as phytoplankton in the form of detritus. In comparison to adult individuals in the Negro River, *S. insignis* juveniles take advantage of a larger diversity of food resources and productivity. This diversity in foraging is important for rapid growth and development before migration to the Negro River at the rising-water stage. Ribeiro (1983) verified that *S. insignis* juveniles do not remain for long in white-water environments, instead moving quickly to the less species-rich blackwater systems in order to avoid predation and/or resource competition with other detritivorous fish species (Saint-Paul *et al.*, 2000).

The Negro River has low primary productivity and few herbaceous plants, which is due to poor nutrient availability, low quantities of suspended sediments (Goulding *et al.*, 1988), and a clay complexation of organic matter that decants to the bottom of the streams and rivers (Leenheer, Santos, 1980). Although periphyton production in this system is lower than vascular plant production, it is the most accessible and available energy source for *S. insignis* adults during the high-water period. The contribution of this source to the adult of *S. insignis* corresponded to the selective feeding of algae in interfluvial wetlands (Junk *et al.*, 2011), where limited plant cover and high light penetration promote periphyton growth (Marshall *et al.*, 2008). Furthermore, inundation of the seasonally-flooded forest with large quantities of decomposing coarse organic matter provides ample substrate for significant colonization of periphytic algae. Vieira (2003) reported that *S. insignis* during the high-water period takes advantage of these opportunities to intensively feed and accumulate fat in both muscle tissue and around inner organs.

Semaprochilodus insignis and other species of the Prochilodontidae and Curimatidae families have been classified by some authors as detritivores/illiophagous or simply illiophagous, which preferably consume epilithon-benthic algae (Fugi, Hahn, 1991; Fugi *et al.*, 1996; Hahn *et al.*, 1998; Almeida, Resende, 2012; Silva, 2016; Doria *et al.*, 2018). Species similar to *S. insignis* in the Prochilodontidae family have small, bristle-like denticles fixed to their lips, which are useful for scraping layers off of sediment and other submerged substrates (Bowen, 1983; Moraes *et al.*, 1997; Guisande *et al.*, 2012). These adaptations allow adult *S. insignis* to exploit fresh colonies of periphytic algae attached to macrophytes (epiphyton) and sediment (epilithon) (Fugi *et al.*, 1996).

Although collections of the autotrophic energy sources were not carried out at the same time as fish sampling, our results provide evidence that *S. insignis* have carved out

a foraging niche that relies predominantly on periphytic algae. In contrast to previous assumptions, we suggest that *S. insignis* present trophic plasticity and changes its dietary regime from detritivorous (juvenile phase) to illiophagous (adult phase) at the same time that it migrates through two liminologically-distinct river systems. *Semaprochilodus insignis* are of great ecological significance for ecosystems because they play an important role in the route of energy flow and nutrient cycling in Amazonian systems. Therefore, more research is needed to better show why this species has such a peculiar behavior and thus elucidate its life history.

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AUTHORS' CONTRIBUTION

Neiliane N. Soares: Data curation, Formal analysis, Writing–original draft, Writing–review and editing.

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ETHICAL STATEMENT

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COMPETING INTERESTS

The authors declare no competing interests.

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